We are most grateful to Dr. James Harrison, Dr. Luc Hoffman and Mr. Alan Johnson for their advice with this note.

Reference:

Blondel, J., (1965). Le Heron cendre, *Ardea cinerea* L., nicheur en Camargue. *L'Oiseau* 35: 59-60.

The tracheae of hybrid Anatidae

by J. V. BEER

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Gray (1958) has listed some 400 inter-specific, inter-generic and even inter-tribal hybrids in the Anatidae, many of which show a remarkable degree of fertility, a characteristic of this family (Johnsgard, 1960a). Their plumage is usually intermediate between that of the parent species but hybrids may also show novel characters or sometimes resemble other species (Harrison, 1953; Harrison & Harrison, 1963; Gillham, Harrison & Harrison 1966; Sage, 1966). The behaviour of hybrids shows a comparable pattern and Sharpe & Johnsgard (1966) consider that both plumage and behavioural characters are under the control of relatively few genes. These features have both evolutionary and taxonomic significance.

The structure of the tracheae of the Anatidae is a valuable taxonomic character (Johnsgard, 1961a) and, despite their diverse form, only one brief comment, in a paper by Harrison (1964), has been found on a trachea from a hybrid.

Hybrid tracheae have been obtained from post-mortem material examined at the Wildfowl Trust, Slimbridge, Gloucestershire, and from material supplied by Mr. J. Hall. Dr. J. M. Harrison loaned several specimens from his museum collection of tracheae.

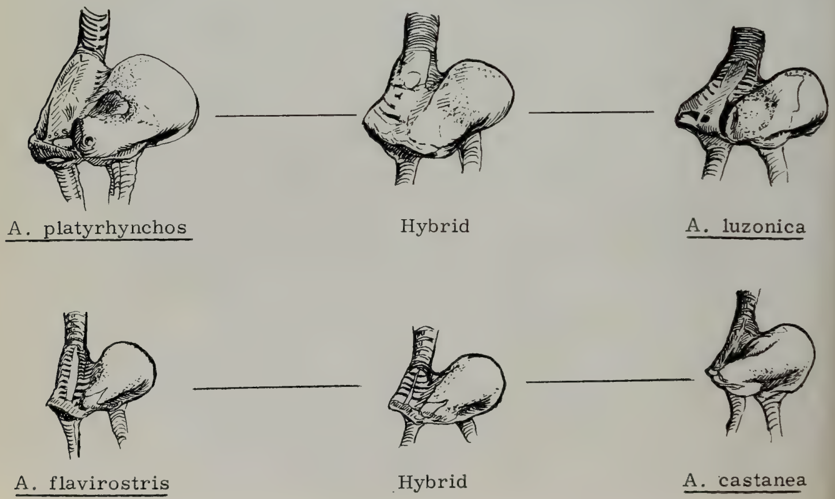


Fig. 1. Syringes of hybrid Anatini—Mallard and teal forms. Ventral view × $\frac{2}{3}$

THE TRACHEA OF THE ANATIDAE

The trachea in the Anatidae is often very distinctive in the males. In some species the width of the tracheal tube varies considerably along its length and in a few species it is convoluted within the sternum or subcutaneously. However, the most interesting feature is the syrinx which in most species has a left lateral enlargement of one of the chambers. This enlargement, or bulla, which is not found in the female, is varied in form and size.

This paper is concerned with a limited number of tracheae from male hybrids of known or putative parentage in the tribes Anatini, Aythyini and Cairinini, all of which show a sexual dimorphism of the syrinx. The nomenclature follows that of Johnsgard (1965).

INTER-SPECIFIC HYBRIDS

Anatini

Crosses studied

Anas platyrhnychos L. Mallard	× *Anas luzonica* Fraser Philipine Duck
Anas flavirostris Vieillot South American Teal	× *Anas castanea* (Eyton) Chestnut Teal
Anas sibilatrix Poeppig Chiloe Wigeon	× *Anas acuta L.* Pintail
Anas penelope L. European Wigeon	× *Anas acuta*
	× *Anas clypeata L.* Common Shoveler
	× *A. sibilatrix*
Anas americana Gmelin American Wigeon	× *Anas falcata* Georgi Falcated Teal
Anas querquedula L. Garganey	× *Anas strepera L.* Gadwall
	× *Anas cyanoptera* Vieillot Cinnamon Teal

platyrhynchos and *luzonica* are typical members of the Anatini and show the characteristic syrinx of the tribe. The latter has the smaller syrinx and the hybrid is intermediate in size (Fig. 1).

flavirostris and *castanea* both have typical anatine tracheae about half the size of *platyrhynchos*. The syrinx of *castanea* is the larger and the hybrid is again intermediate (Fig. 1).

The three wigeons, *sibilatrix*, *penelope* and *americana*, have syringes which differ markedly in size and form and also from that of *platyrhynchos* (Fig. 2). The bulla of *sibilatrix* is large, well rounded and bulbous, but in *acuta* it is smaller and more angular like *platyrhynchos*. The hybrid between *sibilatrix* and *acuta* is intermediate in size and shows some of the roundness of the former (Fig. 2).

The syrinx of *penelope* is smaller than *sibilatrix* and the bulla, though well rounded, is less bulbous (Fig. 2). The hybrid between *penelope* and *acuta* is similar to the previous hybrid but is a little smaller. *clypeata* has a very small syrinx with a reduced bulla that is slightly angular and ovoid

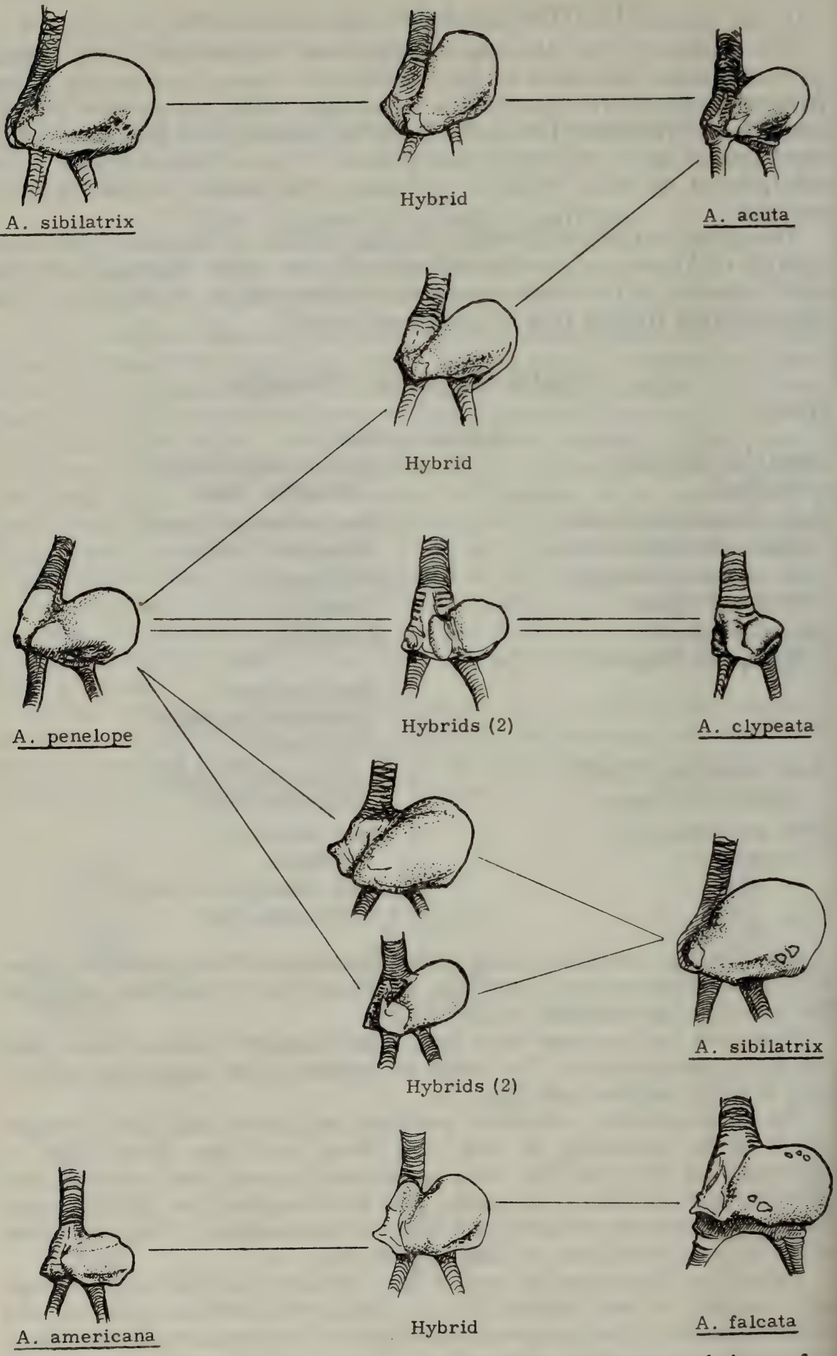


Fig. 2. Syringes of hybrid Anatini—crosses with the wigeons. Ventral view × ⅔

rather than pear shaped. Two hybrid specimens with *penelope*, one from known parents and one from putative parents, are identical. They are a little larger than *clypeata* and show the roundness of *penelope*, giving them a more typical anatine form. Two specimens of a *penelope* × *sibilatrix* hybrid have been seen and in one the bulla is nearest that of the former but is a little larger and slightly more bulbous. However, the second specimen is smaller than either parent but has the same general form of the first.

americana has a small bulla which is not bulbous nor particularly rounded (Fig. 2). The hybrid with a putative *falcata* is intermediate in size and form showing some of the roundness of this parent and the wigeons.

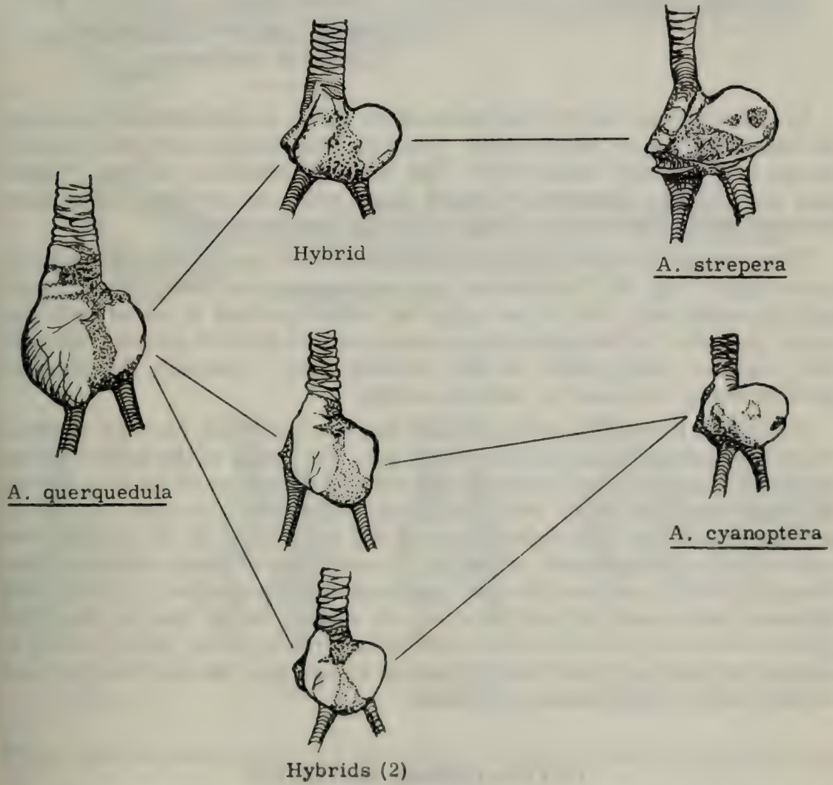


Fig. 3. Syringes of hybrid Anatini—crosses with the Garganey. Ventral view × $\frac{2}{3}$

querquedula has a syrinx which differs from the rest of the Anatini. The bulla is flask shaped (Fig. 3), and lies ventrally over both the bronchi with the larger lobe over the right bronchus. The syrinx of *strepera* is typically anatine but the hybrid, while of similar size to both parents, shows some of the characteristics of *querquedula*. The bulla extends but little to the left, and the right apex, while still between the bronchi, is enlarged and rounded. The small syrinx of *cyanoptera* has the left apex of the bulla displaced posteriorly. The larger of two hybrid specimens, of putative parentage, is intermediate in size and shows the right bullal lobe of *querquedula* and the posterior displaced left lobe of *cyanoptera*. The smaller specimen is similar in form but is nearer in size to the syrinx of *cyanoptera*.

Aythyini

Crosses studied

Netta rufina (Pallas) Red-crested Pochard	× *Netta erythrophthalma* (Wied) Southern Pochard
Aythya ferina (L.) European Pochard	× *Aythya fuligula* (L.) Tufted Duck
	× *Aythya nyroca* (Güldenstädt) Common White-eye

In the Aythyini the tracheal tube often shows a considerable variation in diameter along its length (Figs. 4 and 6). The junction with the syrinx is broad and partially fenestrated. The bulla is relatively narrow, ridged and has slightly fenestrated lateral faces with non-ossified membranes through which the interior of the bulla can readily be seen.

The syringes of *rufina* and *erythrophthalma* are similar but the tracheal tubes differ (Fig. 4). The former has enlargements at both the syringeal and laryngeal ends but in the latter the widest portion is about half-way along the tube. In the hybrid the syrinx is similar to both parents but only the posterior enlargement of the tracheal tube is present, the anterior portion being wide and of uniform width.

ferina has hybridised with *fuligula* and *nyroca* which have no tracheal tube enlargements as in the two *Netta* spp. The width of the tube in *ferina* is greater than in either *fuligula* or *nyroca* and the syrinx of the first species is larger than the other two. The main difference is in the amount of ossification of the right lateral face of the bulla (Fig. 4). In *fuligula* this consists of a fine network, in *ferina* of a wide rim of bone with one large fenestra, while in *nyroca* the face is almost entirely ossified. In the hybrid between *ferina* and *fuligula* the syrinx is slightly larger than in the latter species but the right lateral face is similar in form to *ferina*. In the *ferina* × *nyroca* hybrid the syrinx is intermediate in size and the right lateral face of the bulla is almost entirely ossified.

INTER-TRIBAL HYBRIDS

Anatini × Cairinini

Crosses studied

Anas flavirostris	× *Amazonetta brasiliensis* (Gmelin) Brazilian Teal
	× *Aix sponsa* (L.) North American Wood Duck
Anas sibilatrix	× *Aix sponsa*
	× *Sarkidiornis melanotos* (Pennant) Comb Duck

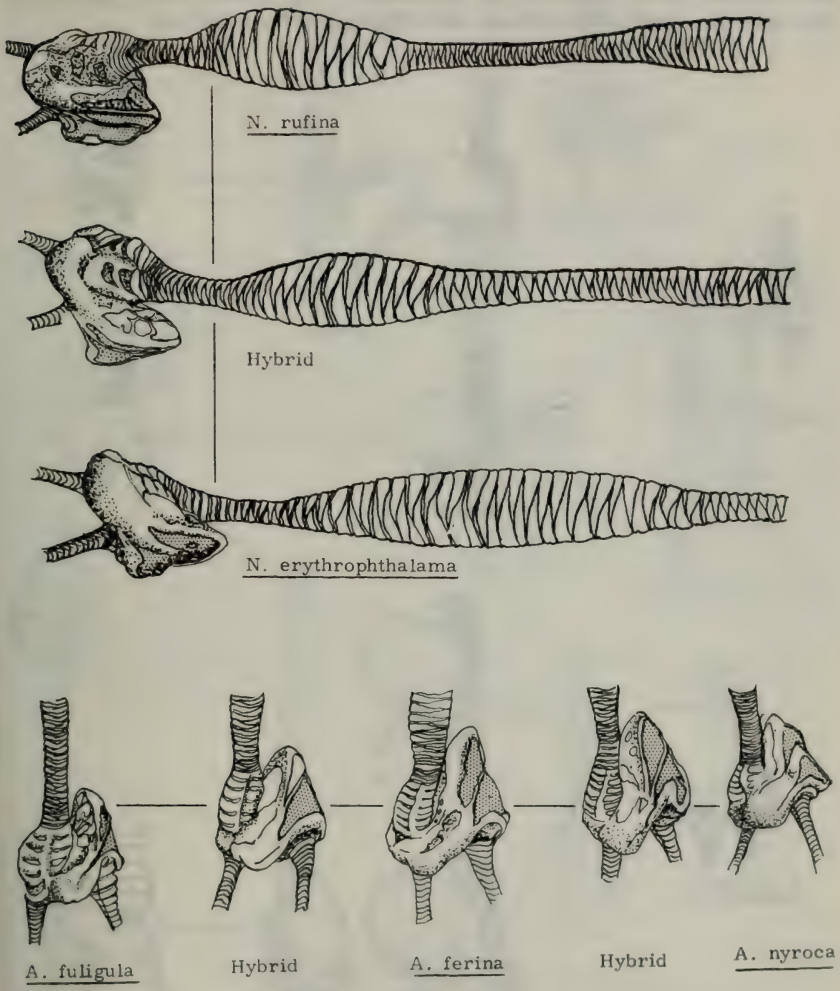


Fig. 4. Tracheae and syringes of hybrid Aythyini—*Netta* crosses and *Aythya* crosses. Ventral view × $\frac{2}{3}$

The general form of the trachea of the Anatini has been described above. In the Cairinini the syrinx is highly variable in size and form. For example in *Nettapus*, spp., the Pygmy Geese, the bulla is extremely small, in *Plectropterus*, the Spur-winged Goose, it is large, discoidal and ossified but thin walled.

brasiliensis has a small syrinx indistinguishable in form from many of the Anatini. The hybrid with *flavirostris* has a syrinx the same size as the latter and is a little more angular but typically anatine in form (Fig. 5). The bulla of *sponsa* is rounded and ovoid with the long axis running from the tracheal tube towards the posterior. The hybrid with *flavirostris* has a globular bulla which shows the influence of both parents.

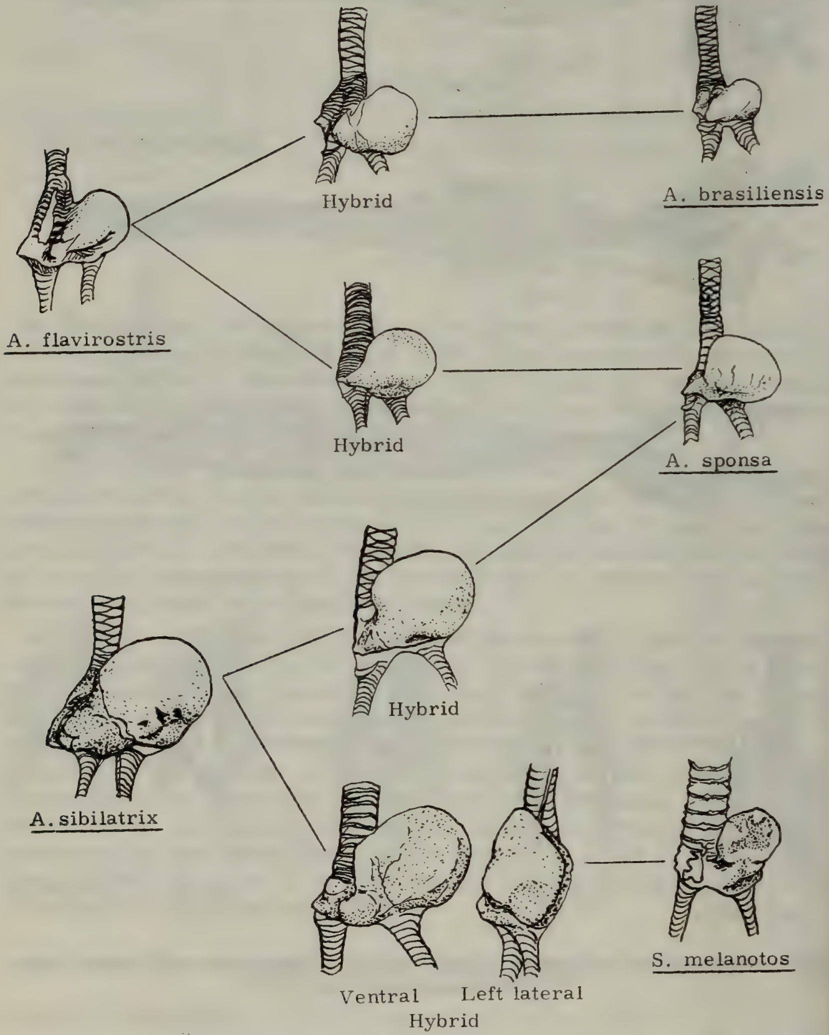


Fig. 5. Syringes of hybrid Anatini x Cairinini. Ventral view × $\frac{2}{3}$

sibilatrix has hybridised with *sponsa* and the hybrid syrinx is intermediate in size, with a well rounded bulla as in *sibilatrix* but with a right hand apex that is large and rounded as in *sponsa* (Fig. 5). *melanotos* has a small, thin walled, irregular discoidal bulla quite unlike *sibilatrix* with which it has hybridised. The hybrid bulla, when seen ventrally, is the same shape as *sibilatrix* but is narrow and discoidal when seen laterally. The degree of ossification is much greater than in *melanotos*.

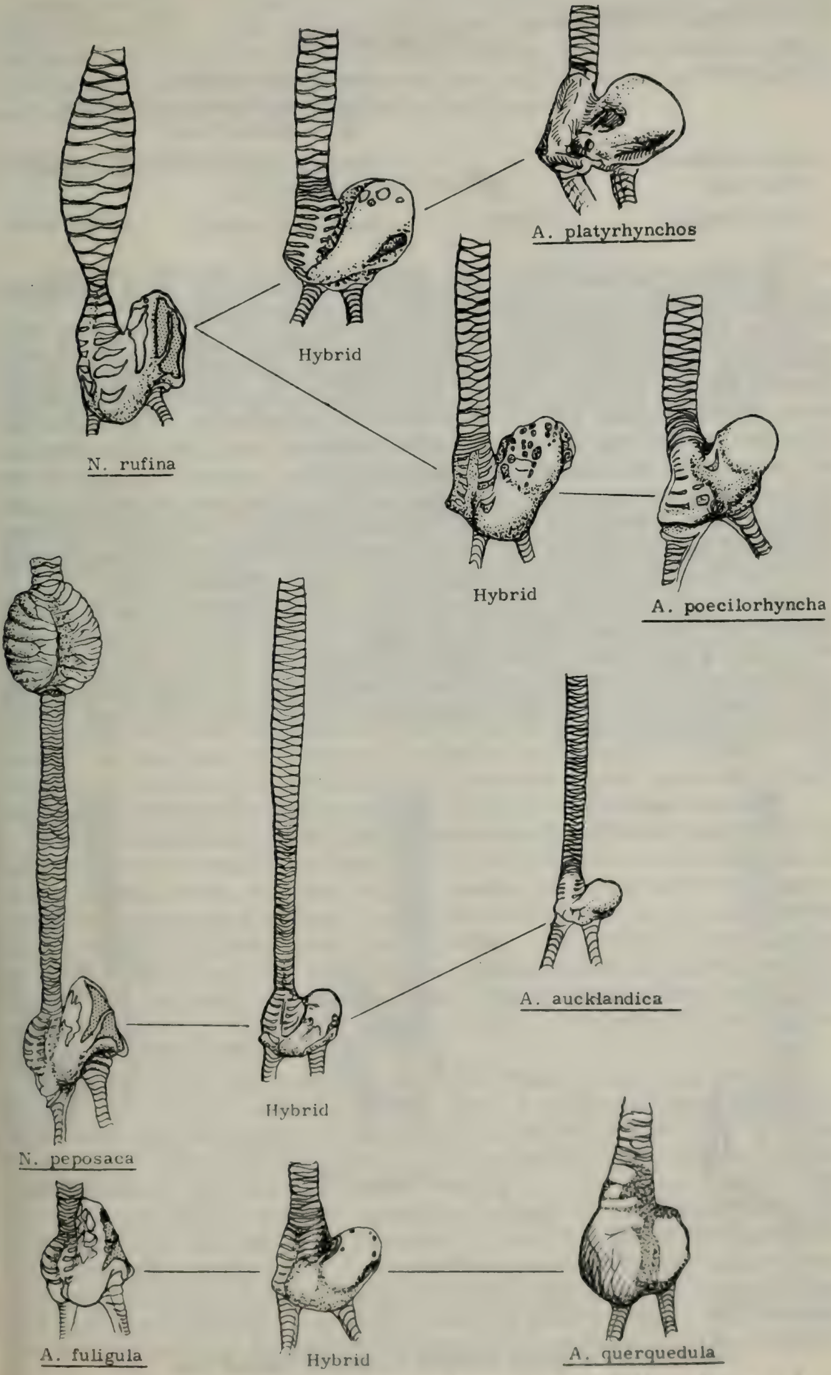


Fig. 6. Tracheae and syringes of hybrid Aythyini x Anatini. Ventral view

Aythyini × Anatini

Crosses studied

Netta rufina × *Anas platyrhynchos*
× *Anas poeciloryhncha* Forster
Spot-billed Duck

Netta peposaca (Vieillot) Rosybill × *Anas aucklandica* (G. R. Gray) Brown Teal

Aythya fuligula × *Anas querquedula*

The hybrids between these two tribes are perhaps the most interesting because of the widely differing forms in the parent species.

rufina has hybridised with two typical species of *Anas*. (Fig. 6). The trachea of the hybrid with *platyrhynchos* is not different in size from the parents but the tracheal tube is a little wider at its anterior and posterior ends reflecting *rufina*. The syrinx is distinctly intermediate with a bulla that is largely ossified and partially rounded reflecting *Anas*. The characteristics of *Netta* show as a narrowing of the bulla with a ventral line near to the tracheal tube, several small fenestrae on the ventral surface and a single medium sized fenestra on each of the lateral faces. In the hybrid between *rufina* and *poecilorhyncha* the bulla is even more angular and fenestrated but otherwise the trachea is similar to that of the previous hybrid.

peposaca has a typical aythyine trachea but the tracheal tube is dilated around the mid-point. This does not show in the hybrid with *aucklandica* which has a small but typical anatine trachea. The hybrid syrinx is intermediate in size and form. It has a broad connection with the tracheal tube and a partially rounded and fenestrated bulla which lies close to the tracheal tube (Fig. 6).

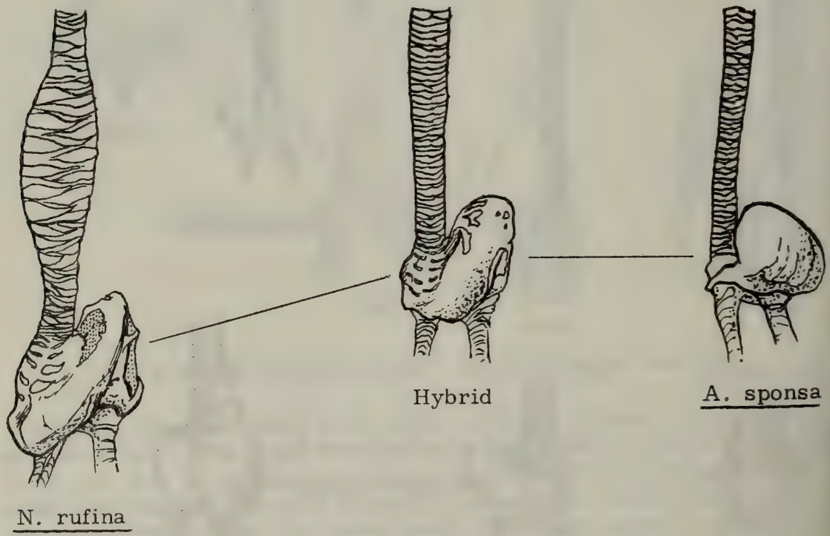


Fig. 7. Syrinx of hybrid Aythyini x Cairinini. Ventral view × $\frac{2}{3}$

fuligula when hybridised with *querquedula* shows a somewhat *Anas* type syrinx but with a broad tracheal tube base intermediate between *Aythya* and *Anas*. The bulla is rounded and intermediate in form between a typical *Anas* and *querquedula*, but there are a few small fenestrae on the ventral surface and a small narrow fenestra on each lateral face.

Aythyini × Cairinini

Cross studied

Netta rufina × *Aix sponsa*

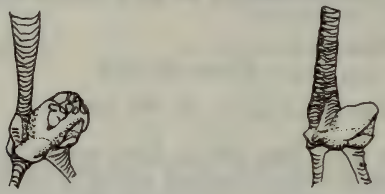
These two species, described above, have very dissimilar tracheae. The hybrid is intermediate in both form and size (Fig. 7). The tracheal tube is a little wider than in *sponsa*, and uniform in diameter, except for a broad base reflecting *rufina*. The bulla is partially ridged with a few small fenestrae simulating *rufina*, the remainder being well ossified as in *sponsa*. The angle of the bulla is like *rufina* but *sponsa* does not show any effect.

DISCUSSION

Most of the hybrid specimens described are intermediate in both form and size which is in keeping with the findings of other workers on hybrid structure and behaviour. The exceptions draw attention to a number of points which must be considered when working with hybrid material. Individuals may differ in size, reciprocal crosses may be different, the genetic make-up will depend on what is available in the genetic pool and the expression of this in the phenotype will depend on the precise genetic structure. A serious problem in much hybrid work is that parentage is often putative, but reasonably accurate assessments can be made using evidence from the history of the bird, its plumage, structure including the trachea, and behaviour. Obviously detailed studies of hybrids require controlled breeding but nevertheless something can be learnt from existing material.

Where the tracheae of the parents are markedly different the influence of both parents can readily be seen in the hybrid, such as when *querquedula* is one of the parents or when *Netta* or *Aythya* is crossed with an *Anas*. In these cases supporting evidence can be provided on the parent composition of a hybrid. In others where the differences are smaller it may still be possible to help assess the identity of a specimen (Beer in Harrison, 1964). In another instance, had all the appropriate specimens been available it might have been possible to have provided further evidence in 'The "Lesser Scaup" problem' (Perrins, 1961).

The syringes of the Anatidae take three main forms, they may lack a bulla, have a fully ossified bulla, or have a bulla with membranaceous fenestrae. *Anas angustirostris* Ménétriès, the Marbled Teal (Fig. 8), has a bulla that is intermediate between the fully ossified type such as *Anas* and the fenestrated type such as *Netta*. Placing it in the genus *Anas* follows Delacour & Mayr's (1945) systematic scheme but Johnsgard (1961b) considers it is not an *Anas* placing it in its own genus *Marmaronetta* (Reichenbach) but retaining it tenatively in the Anatini. He bases this on behaviour and structure including the syrinx, which has an anatine shape but aythyine fenestrae. He considers that the species forms a link between the Anatini and the Aythyini. In his paper on tracheae Johnsgard (1961a) places *Marmaronetta* as a branch on the line leading to *Anas* but near to the branch to the Aythyini. However it is possible that we have an instance of reticulate evolution in which *angustirostris* has evolved from a hybrid between an ancestral species of the Anatini and an ancestral species of the Aythyini. Although many factors operate against the evolution of a new species from an original hybrid (Sibley, 1959) the fact that the Anatini × Aythyini hybrid tracheae bear some resemblance to that of *angustirostris* suggests that this may have happened, which would accord with Johnsgard's assessment of the species' taxonomic position.



A. angustirostris C. leucophrys

Fig. 8. Two further species with fenestrated bullae. Ventral view × ⅔

Fenestration also occurs in other genera, especially those in the Mergini, and in *Calonetta leucophrys* Vieillot, the Ringed Teal (Fig. 8). Several authors (Johnsgard, 1960b) variously consider that this species has affinities with the Anatini, with the Cairinini and with the Aythyini. The true affinities of such abberant species and other species may be more readily assessed if something could be learnt of the evolution of the trachea by the study of hybrids.

Acknowledgments

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References:

Delacour, J. and Mayr, E. 1945. The Family Anatidae. *Wilson Bull.*, 57: 3-55.
Gillham, E., Harrison, J. M. and Harrison, J. G., 1966. A study of certain *Aythya* hybrids. *Rep. Wildf. Tr.* 17: 49-65.
Gray, Annie P., 1958. *Bird Hybrids.* Farnham Royal, Commonwealth Agricultural Bureau, pp. 390.
Harrison, J. M., 1953. On the significance of variations of pattern in birds. *Bull. Brit. Orn. Cl.*, 73: 37-40.
— 1964. Further comments on hybridisation between the European Wigeon and Northern Shoveler. *Bull. Brit. Orn. Cl.* 84: 30-39.
Harrison, J. M. and Harrison, J. G., 1963. A Gadwall with a white neck ring and a review of plumage variants in wildfowl. *Bull. Brit. Orn. Cl.*, 83: 101-108.
Johnsgard, P. A., 1960a. Hybridisation in the Anatidae and its taxonomic implications. *Condor*, 62: 25-33.
— 1960b. The systematic position of the Ringed Teal. *Bull. Brit. Orn. Cl.* 80: 165-167.
— 1961a. Tracheal anatomy of the Anatidae and its taxonomic significance. *Rep. Wildf. Tr.* 12: 58-69.
— 1961b. The systematic position of the Marbled Teal. *Bull. Brit. Orn. Cl.* 81: 37-43.
— 1965. *Handbook of Waterfowl Behaviour.* Ithaca. Cornell University Press. pp. 378.
Perrins, C., 1961. The "Lesser Scaup" problem. *Brit Birds*, 54: 49-54.
Sage, B. L., 1966. A Chilean Pintail x Red-crested Pochard. *Bull. Brit. Orn. Cl.*, 86: 50-54.

Sharpe, R. S. and Johnsgard, P. A., 1966. Inheritance of behavioural characters in F_1 Mallard x Pintail (*Anas platyrhynchos* L. x *Anas acuta* L.) hybrids. *Behaviour*, 27: 259-272.

Sibley, C. G., 1959. Hybridization in birds: taxonomic and evolutionary implications. *Bull. Brit. Orn. Cl.*, 79: 154-158.

Occurrence and behaviour of the Red-footed Booby at Ascension Island, 1962-64

by K. E. L. SIMMONS

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The Red-footed Booby *Sula sula* (Linn) is now very rare at Ascension Island (latitude 7° 57′ South and longitude 14° 22′ West in the Atlantic Ocean), although it probably once nested commonly on the main island until, like the majority of Ascension seabirds, its breeding colonies were extirpated during the nineteenth century mainly by introduced cats (Stonehouse, 1960, 1962). The species was last reported in large numbers in 1946 when Tomlinson (1947) found thousands roosting on inaccessible inland perches on the main island in the vicinity of Powers Peak, White Hill and Weatherpost (see maps in Stonehouse *op. cit.* and in Simmons 1967c for most of the localities mentioned in the present paper). In 1957-59, however, the members of the B.O.U. Centenary Expedition to Ascension failed to find any Red-footed Boobies on the mainland, the only known birds being about ten pairs living on Boatswainbird Island off the south-east coast (in view of Powers Peak, etc.). Only one of these pairs was known to attempt nesting (Dorward 1962a). Ashmole (1963) suggests that the birds seen by Tomlinson ''may have been the survivors from the original Ascension population, long prevented from breeding on the [main] island by the presence of cats'' and possibly too old to breed in 1946; most of them would have reached the end of their life-span between 1946 and 1957 by which time they have been reduced to the tiny, mainly non-breeding remnant on Boatswainbird Island.

SIGHTINGS OF RED-FOOTED BOOBIES IN 1962-64

I was resident on Ascension for two years in 1962-64 and made an intensive study of the Brown Booby *S. leucogaster* (Boddaert) at Stacks 1 and 2 off the north-west coast near the settlement at Georgetown (Simmons 1967b and c). During this time, I saw the Red-footed Booby on a few occasions and was also able to make some useful comparisons between the behaviour of this species and the Brown Booby. These observations seem worth placing on record as possibly the last on *S. sula* at Ascension before its imminent extinction there.

Sightings in 1962-64 were as follows:

(1) brown phase individual with white tail soaring over the mainland near Powers Peak, 17th June, 1962;

(2) white phase bird perched on ground near Powers Peak, collecting nest-material which it took in the direction of Boatswainbird Island, 23rd July, 1962;